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THE CILIARY CURRENTS ASSOCIATED WITH FEEDING, DIGESTION, AND SEDIMENT REMOVAL IN ADULA (BOTULA) FALCATA GOULD 1851 (BIVALVIA, MYTILIDAE)

A Thesis

Presented to

the Faculty of the Department of Biology

University of the Pacific

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Peter Vaughn Fankboner

April 1970

This thesis, written and submitted by

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is approved for recommendation to the

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Dated 18 May 1970

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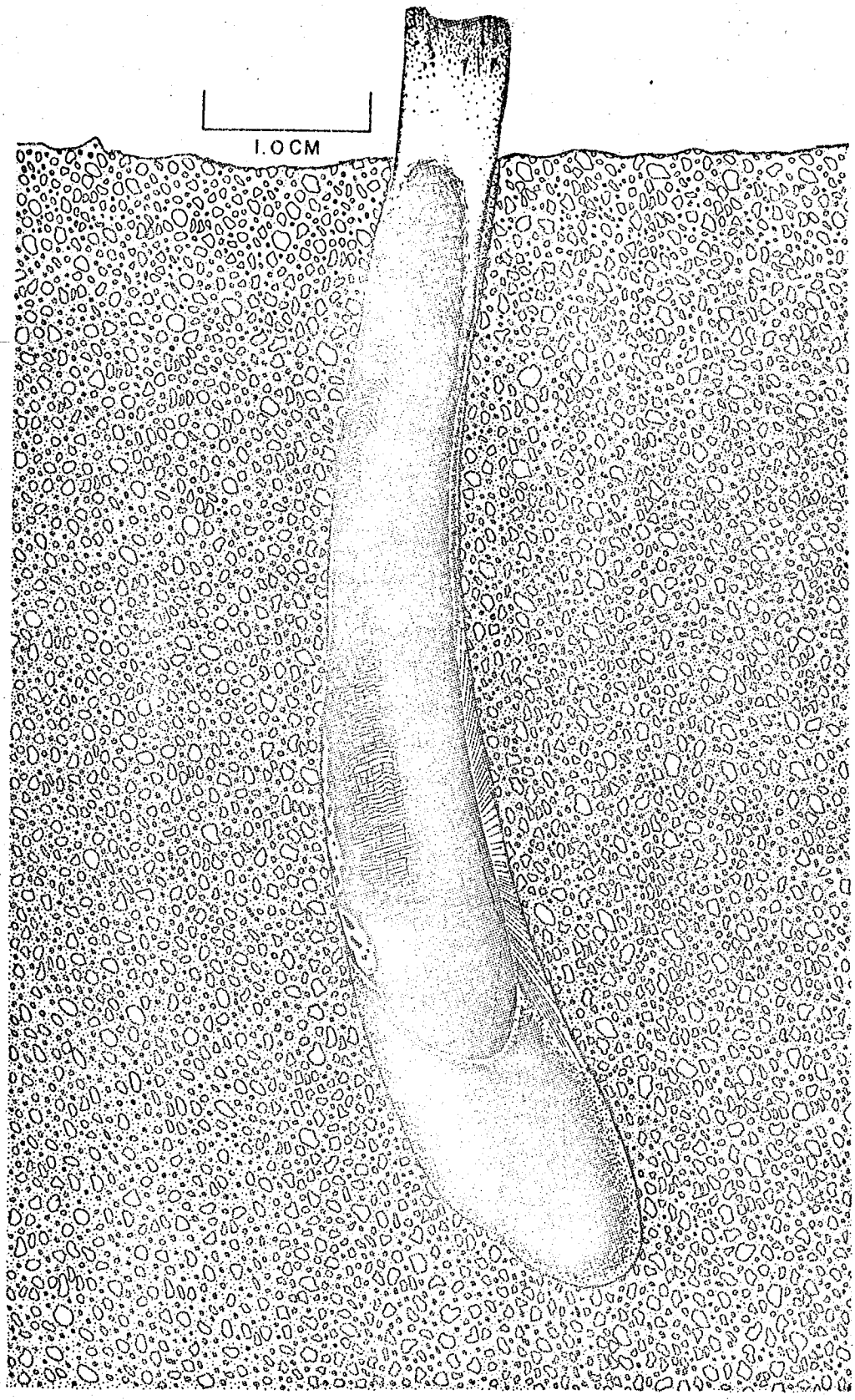
I. INTRODUCTION

Adula (Botula) falcata Gould (Soot-Ryen, 1955) lives commonly as a byssally attached rock borer in soft mudstone reefs at Bolinas and Moss Beach, California (Figure 1). Keen (1963) reports that Adula falcata has been collected from the intertidal to a depth of ten fathoms. Its distribution is from Coos Bay, Oregon, to Cape San Lucas, Lower California (Hertlein and Strong, 1946), and collection data indicate a range as far south as Peru (Soot-Ryen, 1955).

While it possesses the protective advantage of living cryptically, Adula falcata is subjected to an environmental stress not faced by epifaunal mytilids; namely, it must function within a burrow into which sediment material is being continuously deposited from both particle-laden water passing over its burrow entrance and the mudstone byproducts of its own mechanical boring. The following is a comparative study on the ciliary mechanisms of feeding, digestion, and sediment removal in Adula falcata. Sediment removal could hardly be considered separately from feeding and digestion, as it is during these latter two processes that sediment is resolved from potential food material and extruded from the burrow.

Aside from publications of a purely taxonomic nature, the sole direct references to Adula falcata have been in Lloyd's (1897) observations on lamellibranch rock boring and Yonge's (1955) comprehensive work on the adaptation and evolution of the boring habit in the Family Mytilidae. It was, in fact, Yonge's observations on the role of the

Figure 1. A lateral view of the burrow of Adula falcata. The mudstone burrow has been cracked open to expose the left side of the enclosed bivalve. This byssally attached mussel had withdrawn from the head of the excavation and had extended its siphonal process for feeding. Other noteworthy features include the furry incrustation on the posterodorsal triangle of the valve and a partially eroded umbone.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mantle folds during sediment removal from the burrow of Adula falcata which stimulated me to pursue the matter further.

II. METHODS

A clear plastic mold of the burrow was constructed for observing the method employed by Adula falcata for removing the sediment produced during mechanical boring. A piece of mudstone, containing a live specimen of Adula falcata within its burrow, was cracked open and the boring mussel carefully removed. A soap model was made of the burrow and a transparent "Bioplastic" two-piece mold (dorsal and ventral pieces with respect to the orientation of the bivalve) was cast of the soap figure. After the plastic had solidified, and the soap model was removed, the mold was placed under running seawater for several days to remove any traces of water soluble chemicals which might be present on the plastic's surface. Next, the living bivalve, which had been previously taken from the original mudstone burrow, was naturally positioned in the plastic burrow and the bivalve-burrow unit was lowered into running seawater. The bivalve was considered acclimated to the plastic substrate after it had laid down byssal threads on the burrow floor and extended its siphonal process for feeding.

For observations on sediment removal from the burrow, the dorsal half of the plastic burrow was removed and carborundum powder, crushed mudstone, or carmine was placed on the eroded umbones of the specimen's valves. The umbones were selected because they are an

obvious site of mechanical boring. Finally, the top of the plastic burrow was replaced and observations of particle movement were made through the clear plastic by use of a dissecting microscope.

The course of ciliary currents was determined by introducing carborundum #100, carborundum #400, carmine, or crushed mudstone and following the movements of these substances with a Wild M-5 dissecting microscope. The light source used was a 4,000 candle power fiber optics light unit manufactered by Iota Cam Company.

The corrosion-acetate technique, as described by Fankboner (1967), was used for casting the ailimentary tract and the ducts of the digestive diverticula.

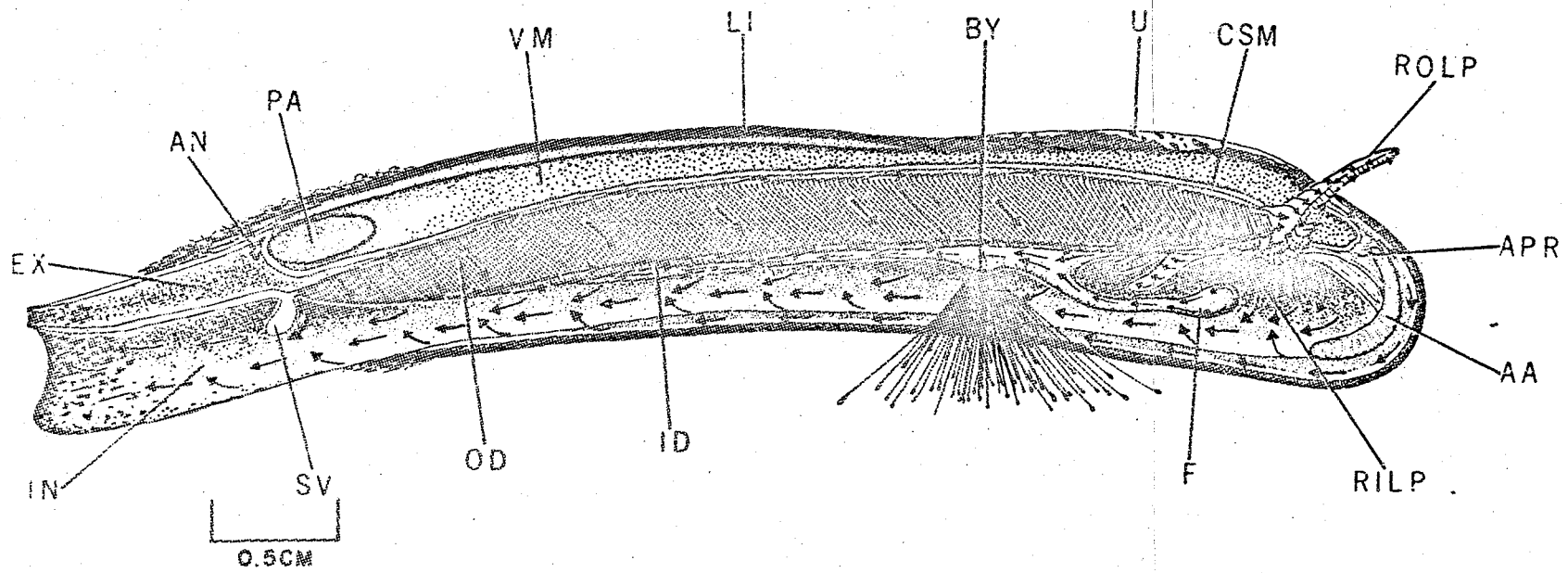
I have attempted to use terminology which is in general use today for description of bivalve functional morphology. Where I have had to give name to a new structure or function will be patent to the reader.

III. THE CILIARY CURRENTS OF FEEDING

The mantle cavity of Adula falcata and its organs are illustrated in Figure 2. This animal feeds in the usual bivalve manner by extending its siphonal process and filtering particle laden water through its ctenidia. An organ of particular interest in the mantle cavity is a flap of tissue extending from the anterior portion of the center siphonal septum, called the siphonal valve (SV). The probable function of this structure will be reviewed in detail in the discussion

Figure 2. The mantle cavity of Adula falcata. The organs and ciliary currents of the mantle cavity are shown after the removal of the right shell valve, the right mantle lobe, and part of the musculature.

AA	anterior adductor
AN	anus
APR	anterior pedal retractor
BY	byssus
CSM	cut surface of the mantle lobe
EX	exhalant siphon
F	foot
ID	inner demibranch
IN	inhalant siphon
LI	ligament
OD	outer demibranch
PA	posterior adductor
RILP	right inner labial palp
ROLP	right outer labial palp
SV	siphonal valve
VM	visceral mass
U	umbone


VM
LI
BY
U
CSM
ROLP
PA
AN
EX
APR
AA
OD
ID
IN
SV
F
RILP
0.5CM

section of this paper.

The gills, or ctenidia, of Adula falcata are heterorhabdic (possessing both principal and ordinary filaments) and eleutherorhabdic (possessing filaments which are not united by organic interfilamentary junctions). However, the gill's filaments maintain a unit integrity because they are bound together in a uniform demibranch by the intermeshed cilia of the ciliary discs (CD) (Figure 3).

Each gill consists of two long, slender demibranchs. The inner demibranch (ID) is complete and lies slightly deeper than the anteriorly reduced outer demibranch (OD) (see Figures 2 and 4). The outer demibranchs are approximately ten filaments shorter at their anterior ends than the inner demibranchs. This condition is not unique to Adula falcata in the Family Mytilidae. I have found a similar reduction of the outer demibranch in Adula californiensis Philippi, Lithophaga bisulcata Orbigny, Musculus (Modiolus) senhousei Benson, and Mytilus edulis Linne´. Stasek (unpublished material) has observed the same condition in Lithophaga plumula Hanley, Musculus (Modiolaria) laevigata Gray, Mytilus californianus Conrad, and Septifer bifurcatus Conrad. A functional advantage for this anatomical reduction is unclear, but, as observed by Purchon (1955a) in discussing Petricola pholadiformis Lamarck (a rock boring eulamellibranch with a reduced outer demibranch), much of the inner demibranch is exposed to the action of the sorting areas of the outer labial palp.

The most anterior filament on the outer demibranch of Adula

Figure 3. A frontal view of the ventral portion of a ctenidial filament of Adula falcata and its ciliary currents. The feathered arrows indicate the path followed by large particles or masses of mucus-bound material. The unfeathered arrows indicate the course taken by the finer, lighter particles.

CD ciliary disc

FC frontal cilia

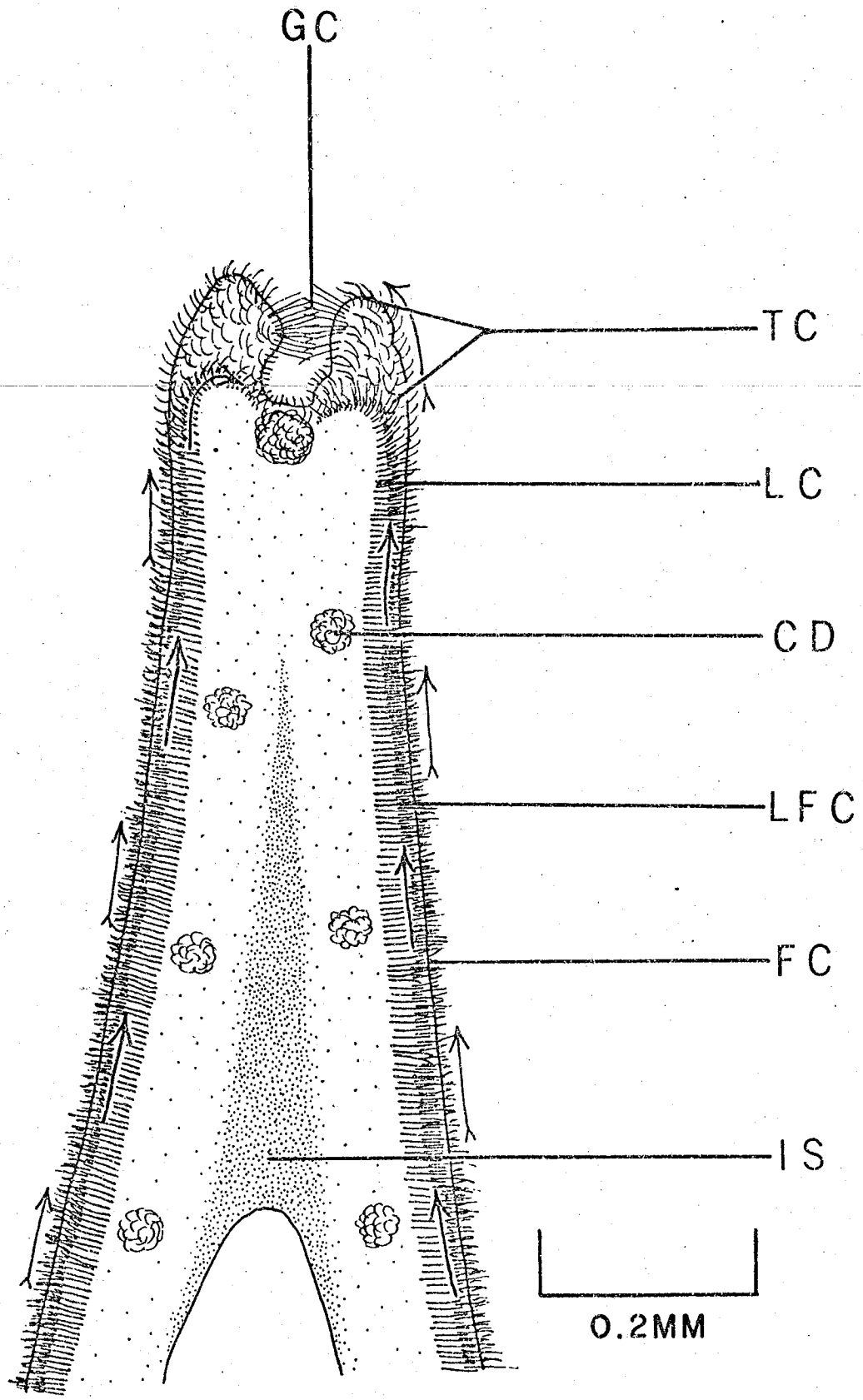
GC guard cilia

IS interlamellar septum

LC lateral cilia

LFC lateral-frontal cilia

TC terminal cilia


GC
TC
LC
CD
LFC
FC
IS
0.2MM

falcata is unusually large and its ventral tip has grown inward, so that it conjoins its terminal food groove with that of the inner demibranch (Figure 4). During feeding, this modified filament passes food strings to the food groove of the inner demibranch which, in turn, conveys them to the palps for further sorting.

The frontal ciliary currents and food grooves of the gills of Adula falcata are similar to those of Atkin's (1937b) category B(1) for the Family Mytilidae (Figure 5).

The first sites of particle sorting on the gills of Adula falcata are the adjacent tracts of fine and coarse frontal cilia (FC) (Figure 2). The fine frontal cilia select the smaller, less dense particles and convey this material ventrally to the food grooves (Figure 3). Once in the food grooves, these particles are passed anteriorly to the distal oral groove (DG) (Figure 4) from where they are later conveyed by cilia to the mouth and ingested. The longer, coarse frontal cilia carry the larger particles and mucus-bound masses ventrally to the tips of the filaments, where they are passed by the terminal cilia (TC) (Figure 3) anteriorly to the palps for further sorting (Figures 4 and 6).

Food material is segregated from unsorted mucus-bound material in the food grooves of the demibranchs by the guard cilia (GC) (Figure 3). The guard cilia originate in the ventro-lateral walls of the food grooves and, from their relative state of low activity, I would conclude that they function as a static barrier to material outside the food grooves rather than mechanically repulsing unwanted material.

Figure 4. The ventral aspect of the ctenidia-palp association in Adula falcata.

DG	distal oral groove
ID	inner demibranch
LG	lateral oral groove
LILP	left inner labial palp
LOLP	left outer labial palp
M	mantle
OD	outer demibranch
PG	proximal oral groove

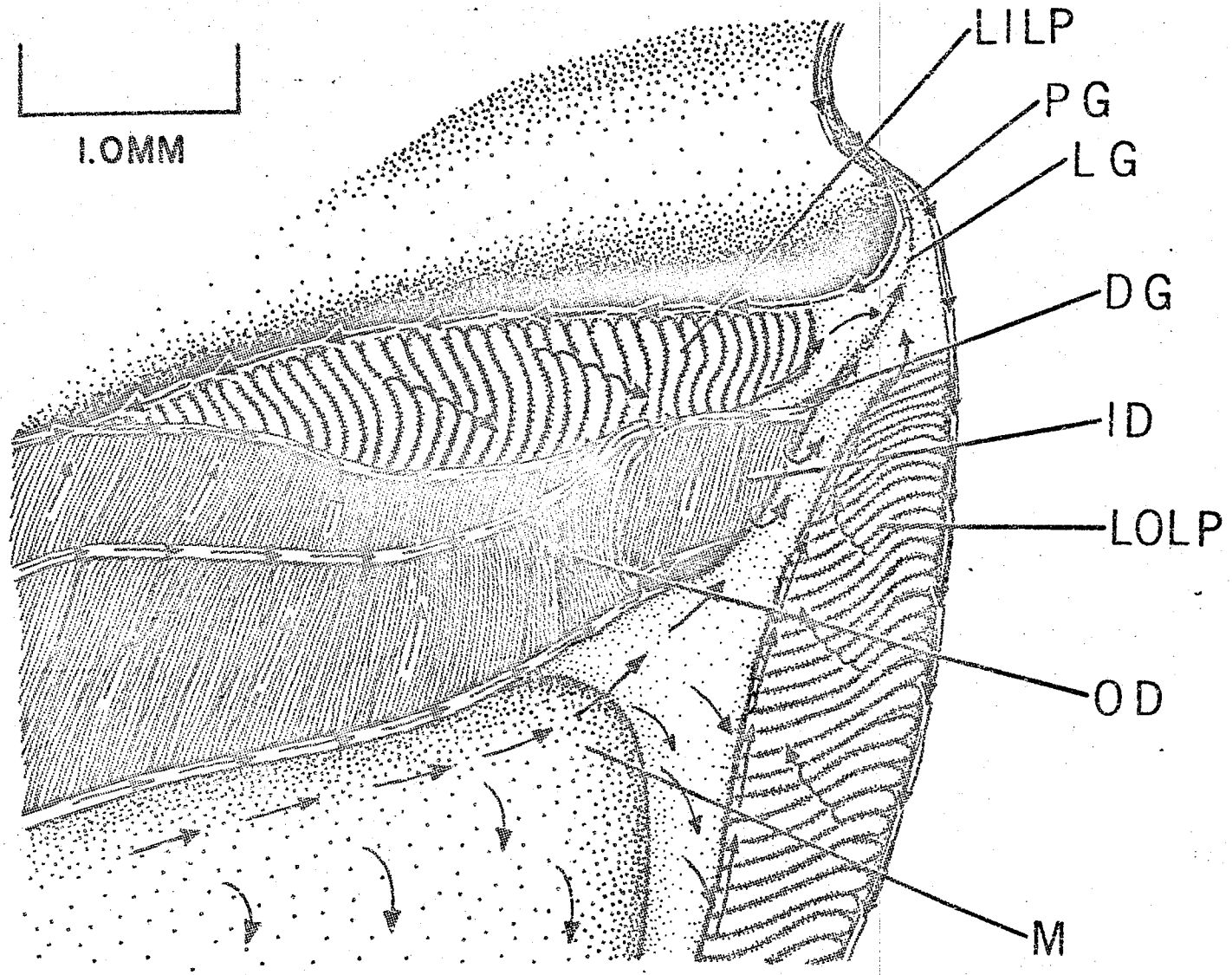

1.0MM
LILP
PG
LG
DG
ID
LOLP
OD
M

Figure 5. A cross sectional diagrammatic representation of the form of the ctenidium of Adula falcata and its frontal ciliary currents. The white stippled areas represent ciliary discs and the arrows indicate the direction of ciliary currents.

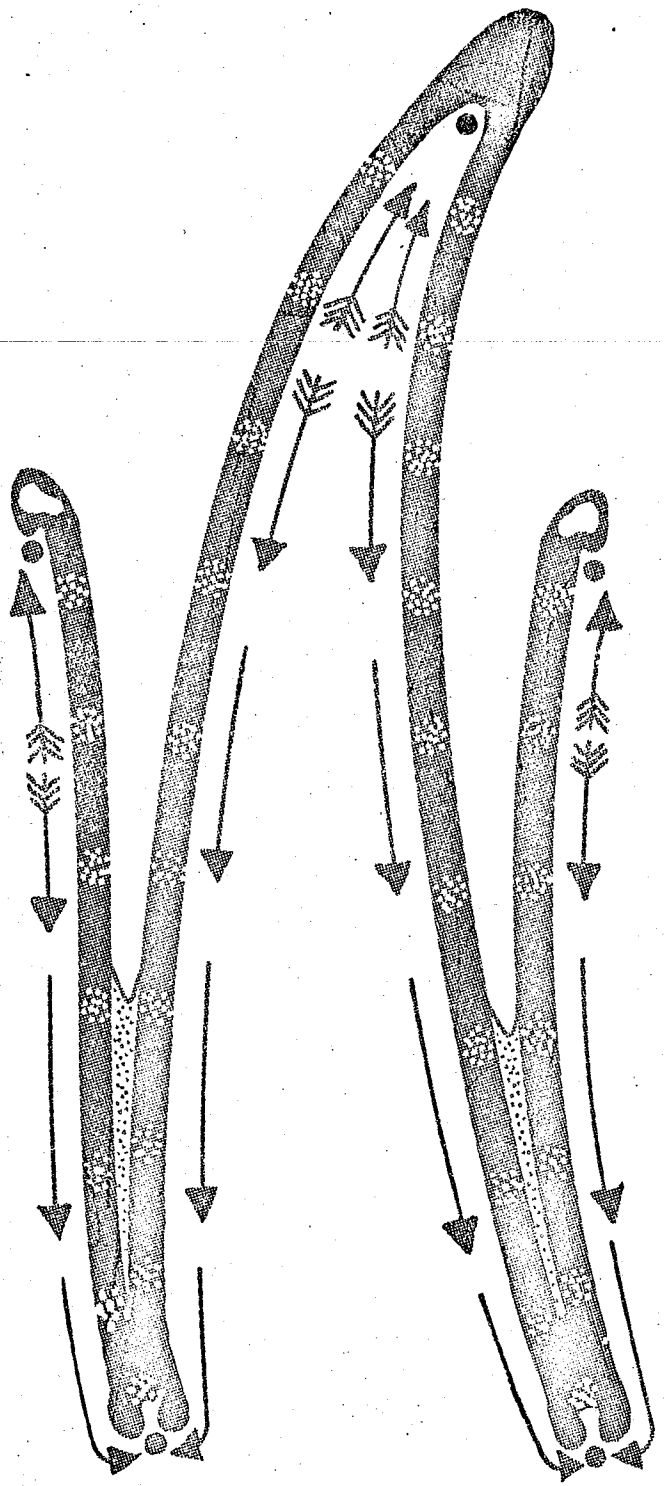
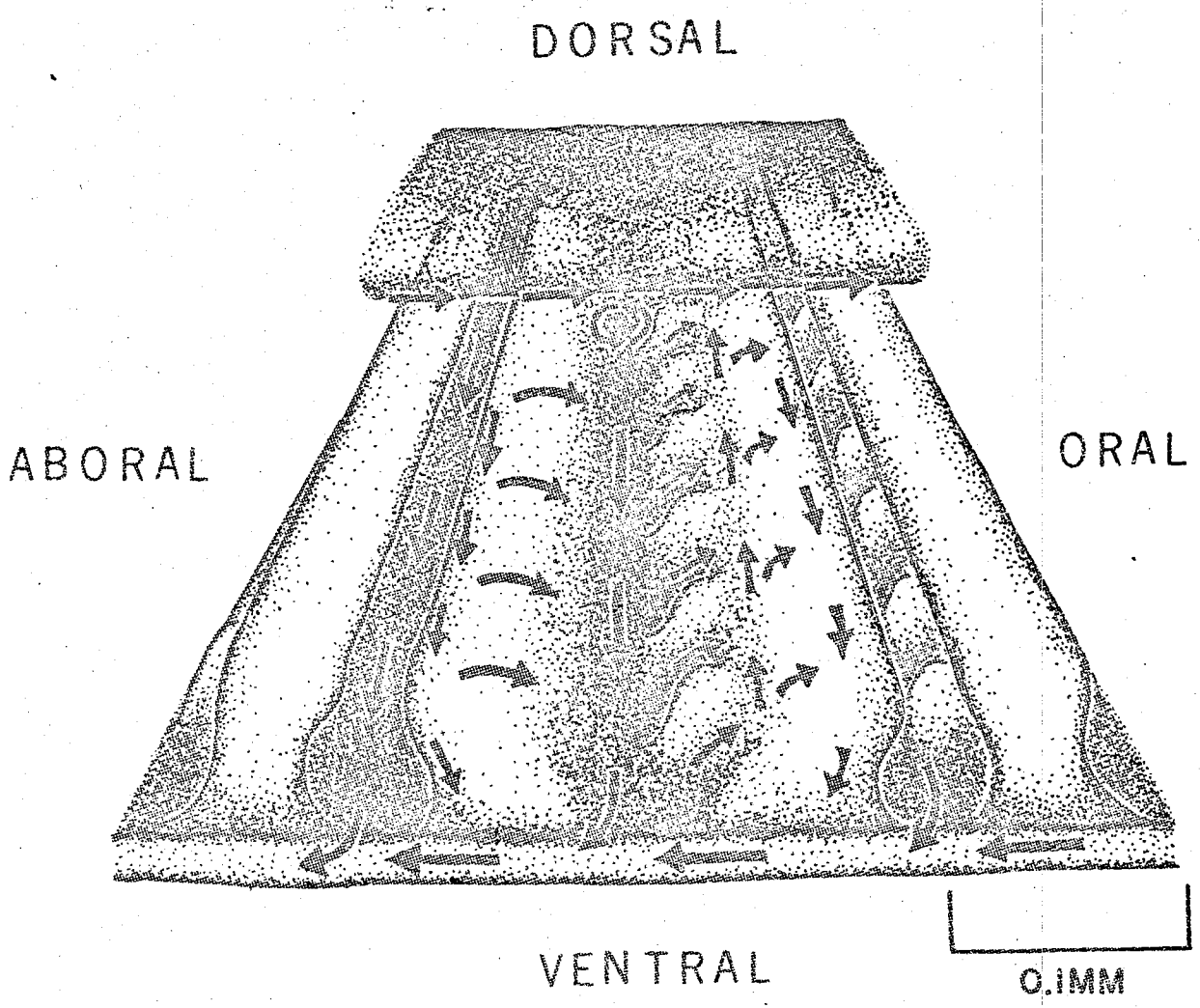


Figure 6. A section of the right inner labial palp of Adula falcata, showing the palp folds and their ciliary currents.


DORSAL
ABORAL
ORAL
VENTRAL
0.1MM

The sorting efficiency of the outer ascending portions of the ctenidial demibranchs is associated with those areas of the mantle wall with which the gills normally come in contact. The ciliary currents of the mantle are essentially those of rejection and, as they are directed ventro-posteriorly, these currents pass at right angles to the ventro-anteriorly directed currents of the ascending portions of the gill's outer demibranchs (Figure 2). This system of ciliary currents produces a ventrally directed resultant vector which will insure that large mucus-bound masses will be rejected as pseudofaeces faster and with more efficiency than by means of the demibranch or the mantle wall alone.

In gross morphology, the paired labial palps of Adula falcata are similar to those described by Kellogg (1915) for Mytilus edulis (Figures 2 and 4). The long, slender palps are quite motile and are generally moving in an exploratory fashion. Where the palps contact the inner surface of the mantle (Figure 2), ciliary tracts on the smooth sides of the palps clean off adhering mucus-bound materials or sediment and convey them to the folds of the palps. Here they undergo sorting (Figures 2 ,4, and 6).

The ciliary currents on the folds of the palps (see Figure 6) are as follows:

1. An orally directed acceptance current passing over the crests of the palp folds.
2. A ventrally directed rejection current moving down the crests of the palp folds.
3. An orally directed acceptance current passing down the proximal slopes of the folds.

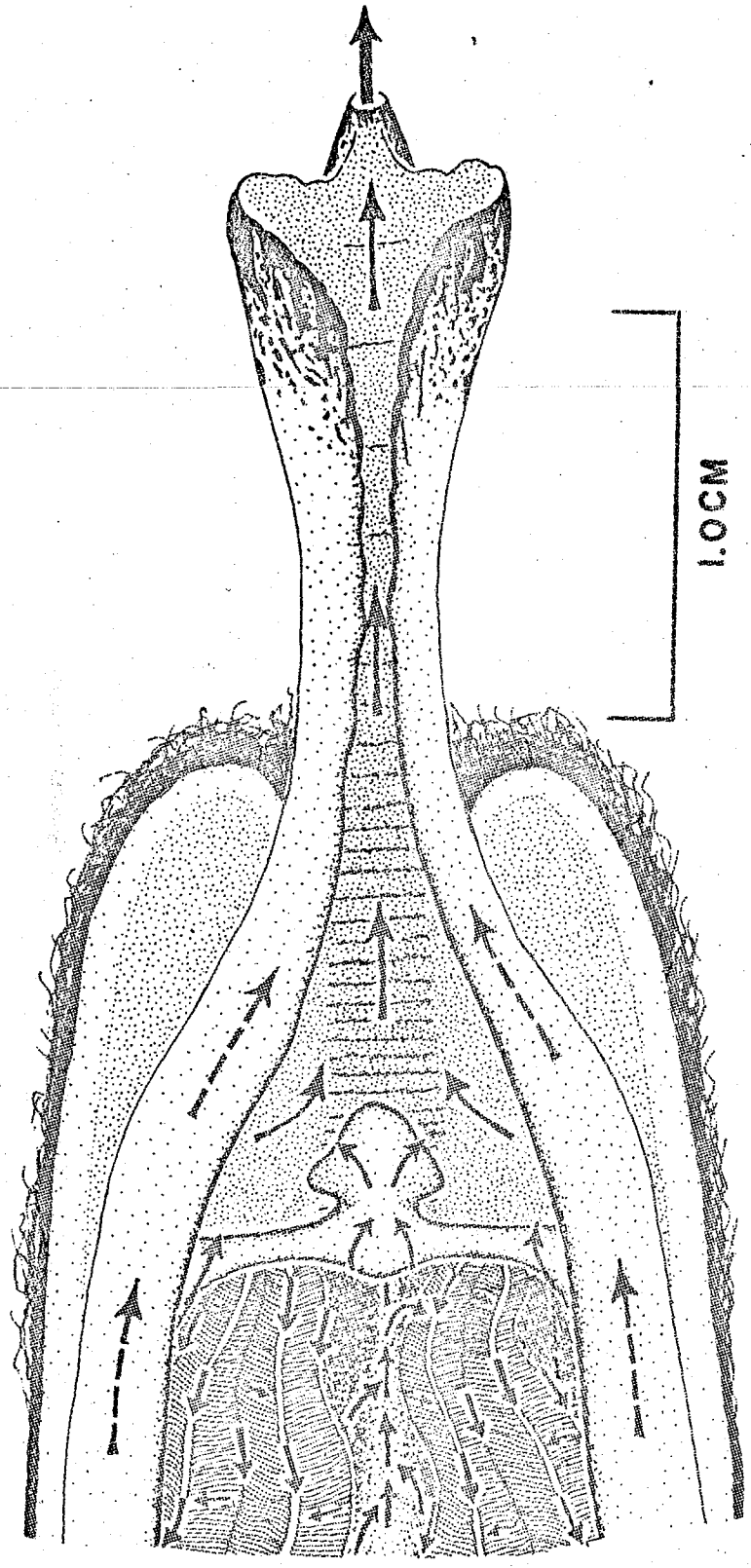
4. A ventrally directed rejection current on the floor of the intrapalp fold groove.
5. An orally directed acceptance current moving up the distal slope of the fold.
6. A dorsally directed resorting current on the upper portion of the distal slope of the fold.
7. A spiraling resorting current between the folds where they insert into the thick portion of the labial palp.

The last mentioned current is probably an accumulative effect of fold currents 3. and 5.

Particles which are accepted by the palps are conveyed orally over the crests of the palp folds or along the margin where the folds insert into the main mass of the palp. Ciliary currents convey this material along the proximal oral groove (PG) (Figure 4) and on to the mouth. Generally, rejected particles are passed directly to the ventral borders of the palps (Figures 2, 4, and 6). This material is collected by cilia lining the inner surface of the mantle lobes or the visceral mass and is carried posteriorly to the embayment of the inhalant siphon (IS) (Figure 7), where it is extruded outside the burrow as pseudofaeces. I have occasionally observed Adula falcata draw the palps across the lips of its mouth in a wiping fashion, leaving particle laden mucus-strings within the proximal oral groove (PG) (Figure 4). This material is ingested by the mouth and conveyed to the stomach, where it undergoes further sorting and digestion.

The primary function of the labial palps of Adula falcata is that of a sorting mechanism, but of almost equal importance is their function as a metering device, controlling, in part, the maximum volume of particles and mucus strings forwarded to the mouth. When this

Figure 7. The ventral aspect of the posterior portion of the mantle cavity in Adula falcata. The valves have been expanded to demonstrate the ciliary currents (solid arrows) of the ctenidia and the inhalant siphon. The dashed arrows indicate the direction of the currents on the inside surface of the mantle-siphon lobes.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volume exceeds the ingestion rate, the mucus strings back up within the oral groove and are rejected by the palps. This excess material either leaves the mantle cavity as pseudofaeces or, more rarely, is accepted by the cilia at the base of the inhalant siphon and returned to the ctenidia for resorting (see Figure 7).

IV. THE CILIARY CURRENTS OF DIGESTION

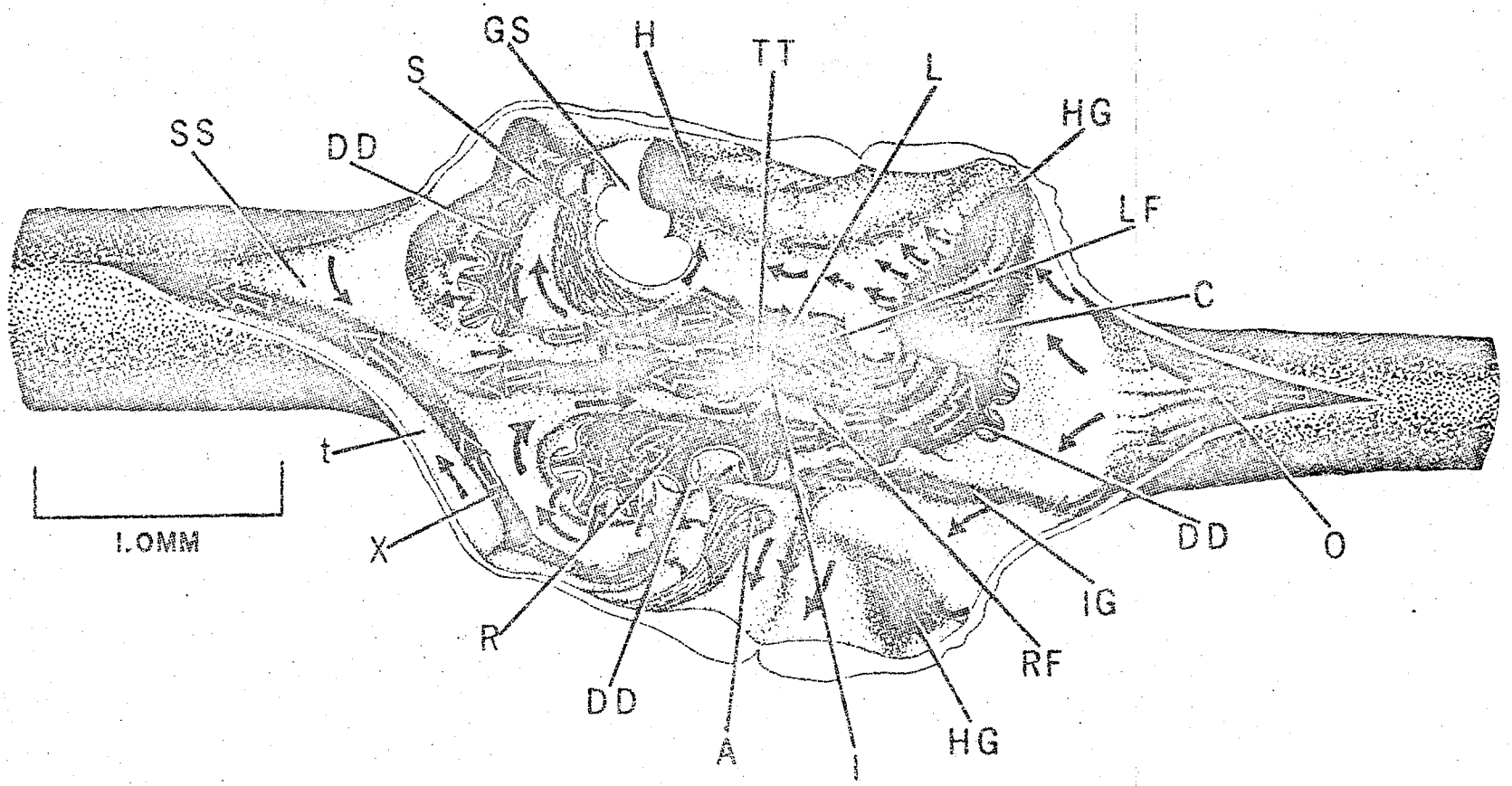
The gut, associated organs, and ciliary currents of Adula falcata are similar to those of Botula cinnamomea (Dinamani, 1967), Mytilus edulis (Graham, 1949, and Reid, 1965), Lithophaga gracilis (Dinamani, 1967), Lithophaga nasuta (Purchon, 1957), and Perna viridis (Dinamani, 1967). However, as there are significant differences between Adula falcata and these other mytilids, I will describe the stomach of Adula falcata in detail and bring out in the discussion section pertinent comparative structures and functions.

In Adula falcata, the short, ciliated oesophagus (OE) leads from the mouth to the spindle shaped mid-gut and its digestive diverticula (DD) complex (Figures 8 and 9). The style sac (SS) terminates just anterior to the posterior adductor (PA), while the intestine forms a long loop by returning to a point just posterior to the right duct pouch and then bends posteriorly and terminates just as it enters the exhalant siphon chamber as the anus (AN) (Figure 2).

The stomach of Adula falcata is a complex sorting organ which houses the entrances to the caecum and the numerous openings to the dichotomies of the digestive diverticula (Figure 8). There are sixteen

Figure 8. The stomach of Adula falcata, its structures, and its ciliary currents.

A	anterodorsal tract
C	caecum
DD	ducts of the digestive diverticula
GS	gastric shield
H	dorsal hood
HG	hood groove
I	intestinal groove
IG	minor intestinal groove
L	left duct tract
LF	left fold of the duct tract
O	oesophagus
R	right duct tract
RF	right fold of the duct tract
S	shield tract
SS	style sac
TT	tongue of the major typhlosole
t	tongue of the minor typhlosole
X	appendix


GS
H
TT
L
S
SS
DD
HG
LF
C
t
1.0MM
X
R
DD
A
I
HG
RF
IG
DD
O

duct openings to the "liver" which are equally segregated into right and left duct pouches (Figures 8 and 9). The ducts and tubules of t digestive diverticula in Adula falcata are similar in morphology and histology to those described by Owen (1955) for Mytilus edulis. The right and left duct pouches in Adula falcata form ciliated gutters along the floor of the stomach which veer to the left anteriorly, entering into the sorting caecum (C) (Figures 8 and 10). The gross ciliary currents of the pouch tracts are towards the caecum.

The caecum (C) is a short, finger-shaped pocket which opens into the stomach upon the left anterior wall (Figure 8). The structure and the ciliary currents of this organ are illustrated in Figure 8, 9, and 10. The sorting mechanism of the caecum in Adula falcata i similar to Reid's (1965) type B classification, with one exception. the blind end of this finger-like pocket is a structure, not found i the caecum of Mytilus edulis, which I call the caecal pouch (CP) (Fi ure 10). This pouch envelopes the terminal end of the caecum's sort folds and appears to physically prevent the larger particles and muc bound mass from entering the hood groove (HG) (Figure 10).

There are four dominant ciliated folds in the stomach of Adul falcata. The shortest of these is the minor typhlosole (t), which enters the lumen of the stomach from the style sac (SS) and extends a short distance along the right wall of the stomach (Figure 8). Th main typhlosole (TT) also originates in the style sac and continues a meandering tongue along the floor of the stomach and disappears in the sorting caecum. Just prior to entering the caecum, it divides u

Figure 9. Drawing of the ventral aspect of a vinyl acetate cast of the alimentary tract of Adula falcata. The duct tubules have been deleted.

C	caecum
L	left duct tract
MG	mid-gut
O	oesophagus
R	right duct tract
SS	style sac

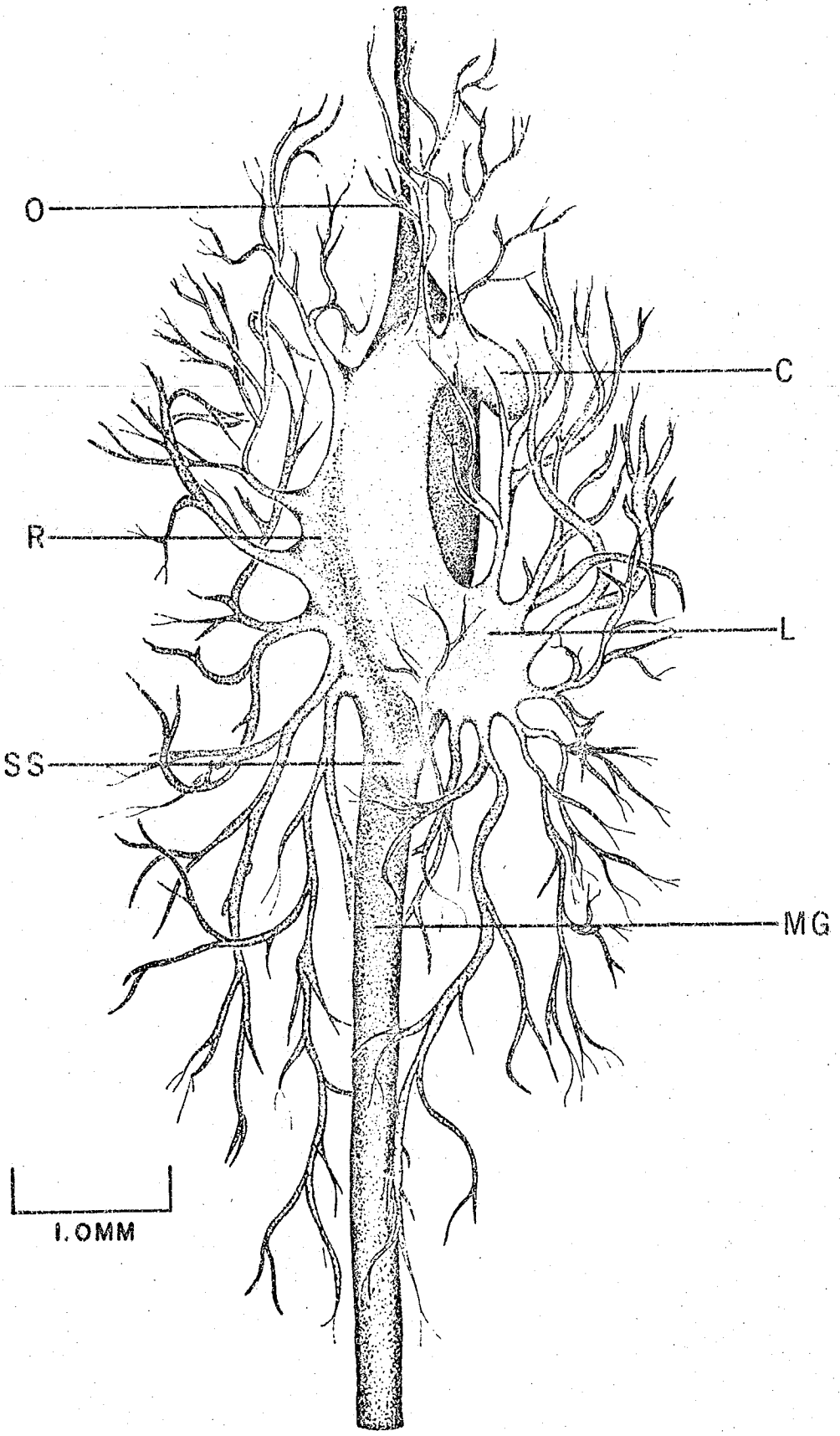
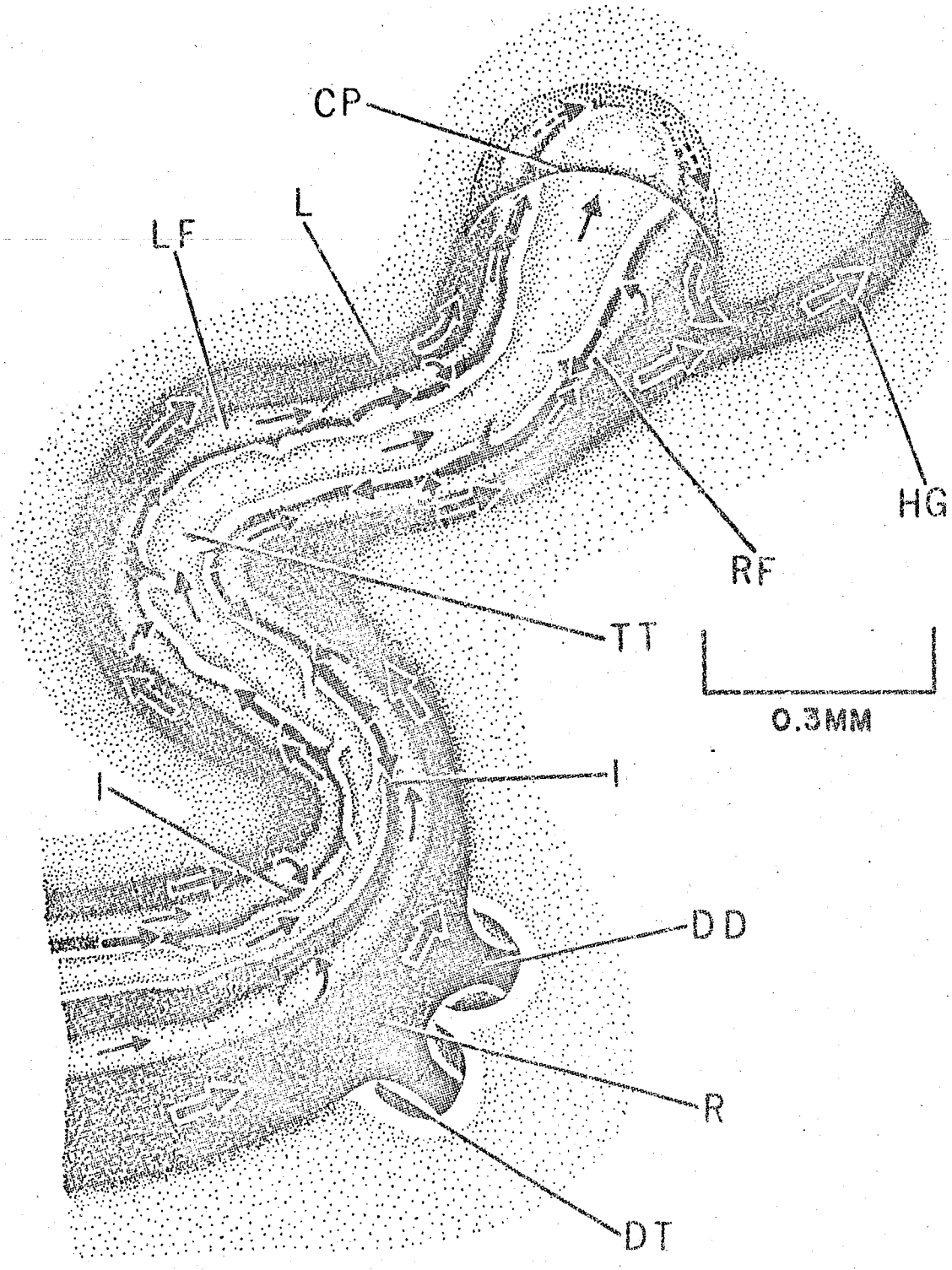

O
C
R
L
SS
MG
1.0MM

Figure 10. The sorting area of the caecum of Adula falcata, its structure, and its ciliary currents.

CP	caecal pocket
DD	duct of the digestive diverticula
DT	duct typhlosole
HG	hood groove
I	intestinal groove
L	left duct tract
LF	left fold of the duct tract
R	right duct tract
RF	right fold of the duct tract
TT	tongue of the major typhlosole


CP
L
LF
HG
RF
TT
0.3MM
I
I
DD
R
DT

qually into two folds. One of these is a continuation of the main typhlosole's tongue, and the other becomes the left fold (LF) of the stomach (Figures 8 and 10). The fourth fold of the stomach, the right fold (RF), has its origin at the base of the right duct pouch and it leads in an anterior direction along the floor of the stomach, finally running parallel to the main typhlosole and following it into the caecum. The reason that I distinguish between a right and left fold is that their ciliary currents run in opposite directions. Also, they lie on opposite sides of the main typhlosole. With the exception of the minor typhlosole, all of these folds convey particles and mucus-bound materials anteriorly into the caecum for sorting.

The intestinal groove (I) has its source at the point where the main typhlosole subdivides to form the left fold of the stomach (Figure 8), and it functions in passing materials, which have been rejected by the sorting mechanisms of the stomach, posteriorly to the mid-gut as waste material.

Forming a tributary to the intestinal groove (I) is a crease in the right wall of the stomach. Its origin is at the oesophageal opening to the stomach and it terminates posteriorly as it joins the intestinal groove. This groove is called the minor intestinal groove (IG) and it has two functions. Its anterior half conveys particles and mucus-bound matter to ciliary currents leading to the dorsal hood; its posterior portion is rejectory in nature and passes rejected materials to the intestinal groove (I) (Figure 8). Just prior to joining the intestinal groove, the minor intestinal groove (IG) forms a shallow

pocket which, in Mytilus edulis, is referred to as the "appendix" (X) by Reid (1965). The function of the appendix in Adula falcata is to remove excess mucus-bound material from the food bolus spinning in the lumen of the stomach. When the bolus becomes too large from a high influx of food material from the oesophagus, it begins to press or extrude the excess into any grooves or pockets within the stomach wall. When such excess material is pushed into the appendix, ciliary currents convey it to the intestinal groove for expulsion from the stomach.

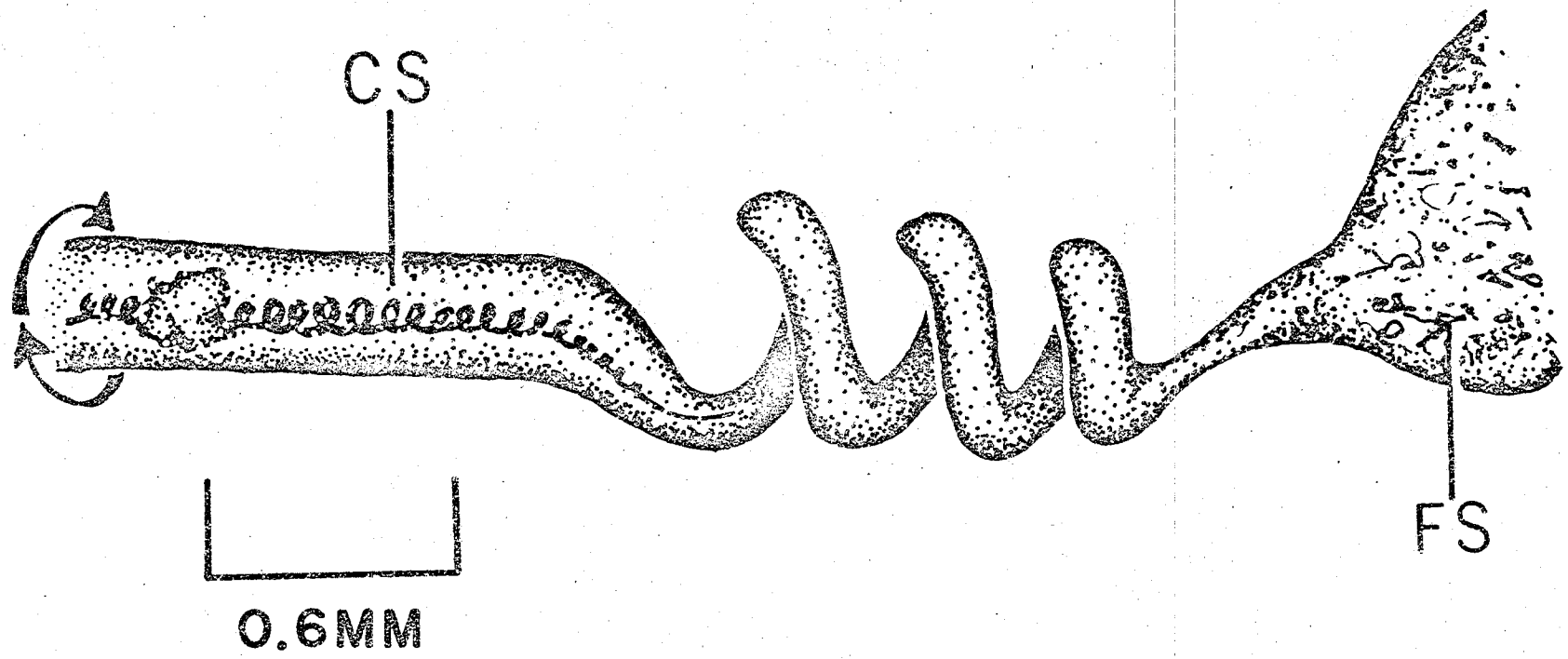
There are two ridged ciliated tracts in the walls of the stomach. One, the shield tract (S) is found on the left wall of the stomach, just prior to the gastric shield (GS). The second, the anterodorsal tract (A), is located on the right wall of the stomach in a position complimentary to the shield tract. The ciliary currents on both tracts are relatively weak and, as far as I have been able to determine, are far less effectual than the other stomach sorting areas. Adula falcata is a relatively advanced member of the Family Mytilidae and quite probably its shield tract and anterodorsal tract have lost the sorting activity observed by Graham (1949) and Reid (1965) in the more primitive Mytilus edulis.

The crystalline style (CS) (Figure 11) projects from the style sac (SS) and its head is lodged against the lobes of the chitinous gastric shield (GS) (Figure 8). In Adula falcata the crystalline style is relatively transparent and has a yellow-orange cast to it. The style's consistancy is very soft and occasionally has little more viscosity than a thick mucus. The soft state of the style is probably

Figure 11. The anterior portion of the crystalline style of Adula falcata. Mucus and food material have been dissected away, showing the dissolving corkscrew-shape of the style tip and the food string to which it is attached.

CS crystalline style

FS food string


CS
FS
0.6MM

due to its intimate contact with materials moving down the intestinal groove. Occasionally, specimens of Adula falcata had styles which contained chunks of food material embedded within the center of the rod (see Figure 11). The presence of embedded matter appeared to be related to whether the animals were freshly broken out of their mudstone burrows and examined in the field or whether they were studied after living in a marine aquarium for several weeks. In the former situation, all of the styles which I examined were clear, but those which were kept submerged and actively feeding in the laboratory tended to develop dark corkscrew spirals of chunky food material down the style centers (Figure 11). The color and texture of these spirals were similar to food strings found in the bivalve's stomach.

The course of digestion begins following ingestion by the mouth of a particle-laden mucus string, which is moved by cilia down the oesophagus and into the stomach. Upon entering the stomach, there are several paths the mucus-food string may take. In Adula falcata, the first of these paths, probably the most frequently used, is similar to that described by Reid (1965) for Mytilus edulis.

The food string is conveyed down the anterior wall of the stomach and is carried in Adula falcata in an oblique direction over the right stomach fold (RF), the main typhlosole (TT), and the left fold (LF). It then passes posteriorly over the left wall of the stomach until it is picked up by the mucus-bound mass enclosing the head of the crystalline style (CS) (Figure 8). The style, which, when viewed from the anterior of the animal, is turning slowly in a clockwise

direction, begins to dissolve and forms a corkscrew (Figure 11) in and around the food-mucus mass. During the spinning of the crystalline style, which is coated with a "bolus" of potential food matter, bits and pieces drop from the turning mucus-bound mass. This is probably due to what Wilbur and Yonge (1967) suggest is the effect of gastric fluids and abrasion by the stomach walls. Most of these food-mucus pieces drop into the right and left duct pouches, where they are either drawn into the main ducts of the digestive diverticula (DD) (Figure 8) or are swept anteriorly into the pouch ciliary tracts and folds for later sorting in the caecum (Figure 10).

Food entering the stomach of Adula falcata at a rate faster than it can sort and utilize it is bypassed to the mid-gut via the intestinal groove. When the mucus-food strings around the head of the crystalline style accumulate to excess, the material is usually scraped off into the appendix (X), where it is later passed to the intestinal groove and carried into the mid-gut as waste.

In the duct pouches, some of the finer particles are taken into the main ducts of the digestive diverticula by what Owen (1955) suggests in Mytilus edulis is an inhalant counter current in the non-ciliated portion of the main ducts, created by an exhalant current in the ciliated portion. The main ducts of the digestive diverticula in Adula falcata were too minute to observe directly the function suggested by Owen. Hence, my observations on ciliary currents of the digestive diverticula were confined to large specimens (8 to 10 inches in length) of Mytilus californianus, which has ducts much larger in

diameter than those of Mytilus edulis. In the larger species, I observed a definite counter current in the main ducts similar to that suggested for Mytilus edulis. The cilia lining the ventral groove in the main ducts of Mytilus californianus beat towards the lumen of the stomach, creating a counter current which flows away from the duct opening towards the secondary ducts. Owen (1955) states that, in Mytilus edulis, the ciliary currents of the main ducts convey waste products from the diverticula to the stomach for removal. He proposes that the counter current functions in drawing food particles towards the diverticula, where they are later digested intracellularly. Adula falcata probably functions in a similar manner.

Those particles which are passed anteriorly in the pouch tracts or in the folds lying on the floor of the stomach undergo minor sorting before they enter the caecum. The smaller, more dense particles are swept off the main typhlosole into the major intestinal groove, to be later passed into the mid-gut as waste material. The larger, mucus-bound masses or strings of material and the smaller, lighter particles are conveyed by the main typhlosole, the pouch folds, and a part of them by the lower left wall of the stomach into the caecum. Once in the caecum, potential food particles are sorted by the right and left folds and the main typhlosole (Figure 10). The heavier, finer particles are rejected into the intestinal groove (I), while the lighter particles are carried into the caecal pocket (CP), where cilia sweep them into the hood groove (HG). Those particles which enter the hood groove are conveyed out of the caecum and to the dorsal hood. At

the head of the dorsal hood, particles and mucus-bound masses accumulate until they spill over the gastric shield (GS) and are picked up by the head of the crystalline style. The larger food strings and mucus masses either remain in the caecum, where they eventually break down into finer sizes, or are passed out of the caecum via the ciliated surface of the caecum's posterior wall. This material is soon caught up in the currents of the stomach's left wall and carried to the head of the dorsal hood. Here it is later wound around the head of the style.

A second path a mucus-food string may take after entering the stomach is to pass along the left anterior wall of the stomach into the caecum. The subsequent treatment of the mucus-food strings within the caecum is similar to that described in previous paragraphs.

The final alternative route which may be taken by mucus-food strings entering the stomach is to be conveyed directly to the minor intestinal groove. Once within this groove, ciliary currents carry the food string posteriorly, where it generally enters the dorsal hood and is passed to the spinning mucus-food mass enveloping the anterior portion of the crystalline style. However, food strings often continue in a posterior direction along the minor intestinal groove. From there they pass into the mid-gut. More frequently, food strings fall into the right duct tract and on to the caecum for sorting.

V. GENERAL COMMENTS ON CRITERIA FOR ACCEPTANCE OR REJECTION OF PARTICULATE MATERIAL BY CILIARY SORTING MECHANISMS IN ADULA FALCATA

Particle selection or rejection taking place in Adula falcata, whether by means of the gills, palps or stomach, appears to be based upon the size, weight, concentration, and mucus-bound state of potential food material. In general, material which is small in size, light in weight, in low concentration, and free of mucus is selected over larger, heavier, highly concentrated, mucus-bound particles (see Table I). I observed no evidence of a selective process other than a physical one.

VI. SEDIMENT REMOVAL FROM THE BURROW

The fate of sediment matter entering the mantle cavity of Adula falcata during feeding has been, in part, previously discussed in the sections of this paper on the ciliary currents of feeding and digestion. Removal of the mudstone breakdown products of mechanical boring from the burrow of Adula falcata is initially a different process, involving active participation by portions of the mantle folds and the foot.

Yonge (1955) has suggested that sediment material resulting from mechanical boring in Adula falcata is removed from the burrow via the folds of the mantle and the inhalant siphon. My observations on a specimen of Adula falcata living in a clear plastic burrow con-

TABLE I

A SUBJECTIVE EVALUATION, BASED ON PERSONAL OBSERVATIONS OF CONDITIONS UNDER WHICH VARIOUS PARTICULATE MATERIALS ARE ACCEPTED BY THE SORTING CILIARY CURRENTS OF THE GILLS, PALPS, AND STOMACH OF ADULA FALCATA

		Carborundum #100	Carborundum #400	Deposited Mudstone	Suspended Mudstone	Carmine
Low concentration	Mucus-bound	-	+	+	++	++
	Mucus-free	+	+	++	++	++
High concentration	Mucus-bound	-	-	+	+	+
	Mucus-free	+	+	+	+	+

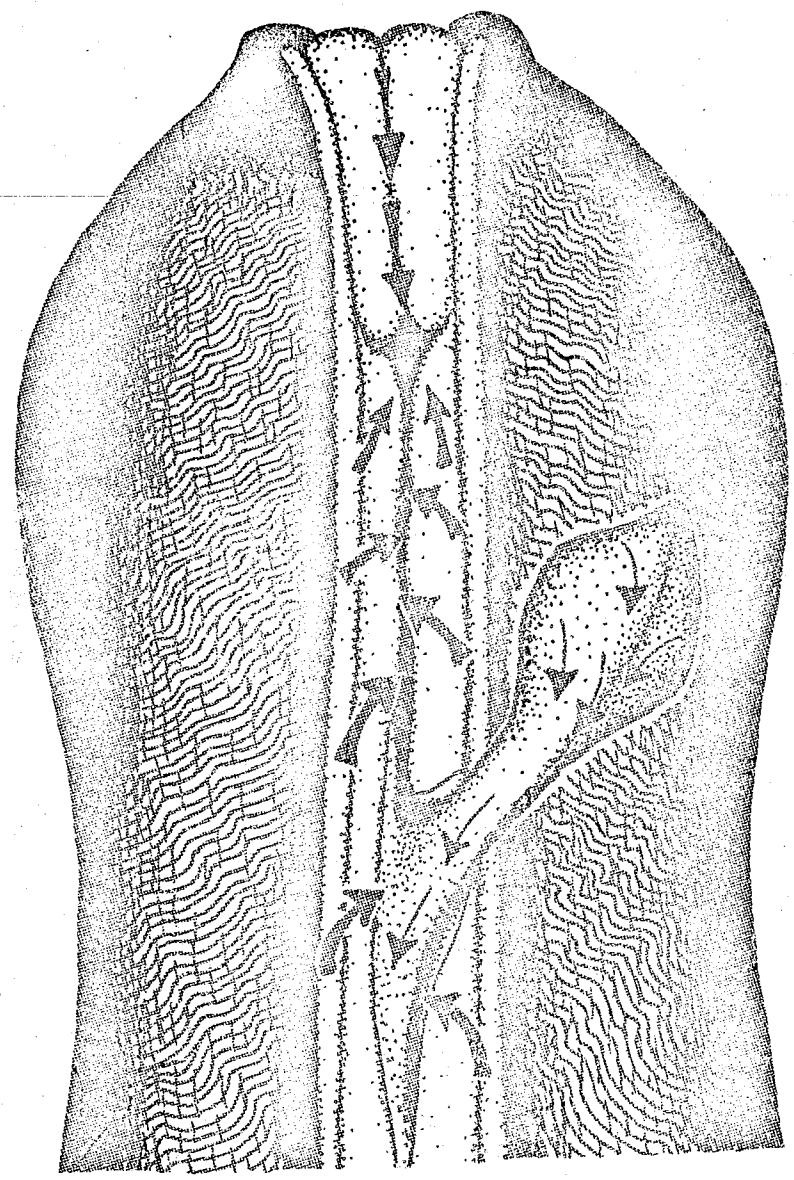
\- = None accepted

\+ = Little accepted

++ = Most accepted

firm this. The larger particles, such as carborundum powder #100 and #400, which I placed on the umbones of the specimen in the plastic burrow, were deposited within a few minutes at the head of the burrow. (The burrows of Adula falcata are usually positioned vertically in mudstone reefs, as shown in Figure 1.) The deposited particles were contacted by the anterior fused inner folds of the mantle margin and conveyed by cilia ventrally (with respect to the bivalve) and passed into the lumen of the mantle cavity (Figures 3 and 12). If the carborundum particles entering the mantle cavity were introduced in large quantities, they generally became embedded in the mucus produced by the mantle epithelium and were conveyed as stringy masses posteriorly by cilia lining the walls of the mantle cavity. On reaching the inhalant siphonal embayment, the mucus-bound particles were swept away by the currents of the exhalant siphon (see Figure 7). Wave action on the reef probably carries the mucus-embedded material a considerable distance from the burrow opening before it breaks up. Hence, it is unlikely that the material would be introduced again in the feeding process. When small quantities of carborundum particles were taken into the mantle cavity, they were usually conveyed to the sorting folds of the labial palps, where they were treated like incoming potential food material. Finer suspended particles in the burrow are drawn into the mantle cavity through an iris-like opening formed by the anterior unfused portion of the ventral mantle marginal folds (see Figure 12). The water currents which draw in this suspended material are probably created by the slight

Figure 12. The ventral aspect of the anterior portion of Adula falcata, showing the folds of the mantle, the foot, and their ciliary currents.



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opening and closing of the shell valves because the fluids were taken into the mantle cavity in gasping draughts, rather than in the steady flow characteristic of ctenidial currents. After suspended material has entered the mantle cavity, it is collected by the filtering mechanism of the gills and processed as potential food material.

The foot of Adula falcata is long, slender, and serpentine in its movements and shape. Yonge (1955, p. 387) submits: "Once the animal is established in its boring the only, but all-important, function of the foot is to plant the byssus threads." My observations have revealed that the foot (F) (Figure 2) of Adula falcata has a significant additional function, that of removing sediment from the walls of its mudstone burrow.

The ciliary currents of the foot of Adula falcata are shown in Figures 2 and 12. The extensible powers of the foot are unusual. I have on occasion observed it expanded to at least four-fifths the length of the shell valves. There does not appear to be any portion of the walls of the mudstone burrow or of the shell valves which is inaccessible to the tip of the foot. Observations on Adula falcata in the clear plastic burrow revealed that the foot occasionally extended and touched portions of the burrow walls in a browsing manner. Further, wherever the ciliated foot touched areas of the burrow walls which were coated with #400 mesh carborundum powder, the particles were removed and passed to the mantle cavity by the foot's ciliated surfaces.

Mudstone particles and carmine were substituted for carborundum

powder during observations on sediment removal and appeared to be treated in the same way by Adula falcata: according to particle size, particle density, and mucus-bound state. I was never able to place more particulate material within the plastic burrow than could be handled by the mantle cavity's mechanisms for sediment removal. I was particularly impressed with the ease with which the ciliary currents of the inhalant siphon could move large, dense, mucus-bound masses (sometimes 0.5 centimeters in diameter) of #100 mesh carborundum powder in a vertical direction. In general, large particles were removed from the burrow as pseudofaeces via the inhalant siphon. Smaller, suspended material entered the alimentary system and was incorporated into faecal pellets. On occasion, some of the faecal pellets produced strongly evidenced the carmine and carborundum particles administered during studies of sediment removal. However, there is little doubt that ciliary rejection mechanisms in the mantle cavity play the most significant role in the removal of sediment particles from the burrow.

VII. DISCUSSION

In particle laden waters, many eulamellibranchs rid their mantle cavities of clogging particles by first concentrating the undesirable material into mucus-bound masses at the base of the inhalant siphon and by then directing the siphonal valves so that the incurrent stream of water washes the pseudofaeces from the mantle cavity ventrally through the gape in the mantle margins (Kellogg, 1915). It is

manifest that a rock boring form such as Adula falcata can not utilize the above mechanism because it would result in effectively "fouling one's own nest". Kellogg (1915) and Purchon (1955) have noted that members of the genus Barnea have evolved a filmy flap, called a collecting membrane, which extends from the posteroventral portion of the visceral mass deep into the inhalant siphonal embayment. Posteriorly directed ciliary currents of the collecting membrane deposit pseudofaeces into the incurrent siphon, where it is removed from the bivalve via extrusion through the siphon's opening. Such a system bypasses the problem of the stream of incoming water washing away the pseudofaeces because it effectively shields the material until it is deposited near the point of extrusion. Yonge (1955) suggests that the siphonal valve (SV) (Figures 2 and 7) of Adula falcata acts as a shield to protect pseudofaeces from the broad incoming stream of water from the inhalant siphon. I question this interpretation for two reasons. First, any material passing posteriorly through the inhalant siphon would obviously be subjected to the full force of the incoming water currents when it was carried by cilia over the siphonal membrane or the inner walls of the anterior portion of the mantle folds (Figure 7). Second, Adula falcata utilizes a gape in the ventral mantle folds just anterior to the siphonal process as a functional inhalant siphon during the removal of moderate to heavy loads of sediment and pseudofaeces. While this "functional" inhalant siphon is operative, the siphonal valve appears to work as a plug for the true siphon.

Guard cilia generally occur in those bivalves which inhabit a substrate containing some muddy or silty material (Atkins, 1937a). The mudstone burrow of Adula falcata provides a similar habitat because sediment material from both mechanical boring, within the burrow, and suspended silt from mudstone weathering, outside the burrow, are deposited into the excavation. The deep marginal grooves and their guard cilia provide a mechanism in Adula falcata for insuring that potential food material travels the full distance to the labial palps, while at the same time remaining segregated from the silt laden stream of water entering through the inhalant siphon.

Stasek (1963) has determined, from fifty-five bivalve families, that a well defined association is present between the ctenidium and the labial palps. Based on anatomical characters, he has segregated members of these families into three major categories. As a mytilid, Adula falcata would fall into the most primitive of these groups, Category I.

Members of Category I are characterized by Stasek (1963) as having the following anatomical features: " . . . the ventral tips of at least the first few or, usually, of many filaments of the inner demibranch are inserted unfused into a distal oral groove (a designation originated by Kellogg, 1915)." In Adula falcata and, indeed, in all of the Mytilidae I have examined, the first few filaments of the inner demibranch are inserted unfused into a palp pocket lying within the lateral oral groove (LG) (see Figure 4). Kellogg's (1915, p. 629) definition of the distal oral groove states (the italics are mine):

"The third is a groove in the mantle wall, close to, and paralled with, the anterior edge of the inner demibranch, found in forms in which the outer demibranch does not extend so far forward as the inner--the distal oral groove." Kellogg further submits that there is no distal oral groove in Mytilus, and he is correct on the basis of his purely anatomical definition. However, Stasek (personal communication) feels that, in the Mytilidae, a functional basis for a ctenidium-palp association is more valid than a purely anatomical one. While I agree with Stasek on this point, I think that his definition for Category I would be more convincing if it read as follows: " . . . the ventral tips of at least the first few or, usually, of many filaments of the inner demibranch are inserted unfused into an anatomical or functional distal oral groove."

The stomach of Adula falcata is well equipped to handle the fine sediment particles accompanying incoming food material. It differs from other mytilian rock borers, such as Botula cinnamomea and Lithophaga gracilis (Dinamani, 1967), in that it possesses a well-developed sorting caecum. The folds and typhlosolar tongue of the caecum of Adula falcata comprise the chief sorting mechanism of the stomach, as the anterodorsal and shield tracts appear to be ineffectual. Those sediment particles which get by the sorting mechanisms of the ctenidia and labial palps and which are conveyed to the stomach of Adula falcata are generally dealt with by the caecum and dumped into the intestinal groove, to be carried out of the region of the stomach. The absence of a well-developed caecum in Lithophaga gracilis

might be related to the chemical nature of its boring. Lithophaga spp. are usually found burrowed in a limestone substrate (Yonge, 1955) and, during the boring process, do not produce a particulate sediment. Hence, they probably do not require the sorting mechanism found in Adula falcata.

Dinamani (1967) has suggested that the caecum functions more as a temporary reservoir of food than as a sorting mechanism in the Mytilidae. He observed that, in specimens of Perna viridis starved for up to two days, the food matter within the caecum had disappeared. The caecum may have a purely storage function in mytilids where the sorting folds of the caecum are rudimentary,such as in Botula cinnamomea, Lithophaga gracilis, and Perna viridis, but in Adula falcata and Mytilus edulis, where the sorting mechanism is well-developed, the caecum is patently a device for resolving food matter from mucus and sediment particles.

The complexity and functional significance of the appendix in the bivalve stomach ranges from a rudimentary, static groove in Mytilus edulis (Reid, 1965) to the large food storage pouch found in the wood-boring Teredinidae (Purchon, 1968). Yonge (1949) submits that the appendix or the anterodorsal caecum in tellinids functions as both a storage cavity for sand grains to aid in trituration of food material and a relief valve for excess food-mucus strings accumulating around the head of the crystalline style. The rejectory currents of the appendix of Adula falcata preclude its functioning in a storage capacity. Moreover, I was never able to observe the overt abstraction of

mudstone particles in any portion of the stomach. The appendix of Adula falcata functions solely as a relief mechanism, and, instead of temporarily storing the bolus material pressed into it, the ciliary currents of the appendix convey it to the intestinal groove, where it is subsequently removed from the stomach. The obvious advantage of the appendix to Adula falcata is that the presence of a relief mechanism in the stomach prevents overeating and, thus, maintains the proper volume for optimal mixing of food with gastric juices.

The crystalline style from specimens of Adula falcata maintained in aquaria often contained bits and pieces of food matter. Morton (1952) suggests that this is a common occurance which is advantageous to the style bearer in that it permits recovery and digestion of food matter which would otherwise be lost as faeces. Nelson (1918) found similar structures in the styles of Anodonta grandis and Modiolus modiolus yet stated that these animals had been freshly collected. Nelson's explanation for this phenomenon was that, during the formation of the crystalline style, a clear mucus string is secreted by the walls of the intestine and picked up by the ciliated faces of the typhlosoles in the mid-gut. During the process of the mucus string's being carried to the typhlosoles, it is twisted on itself and forms a corkscrew spiral. Frequently, odd particles of food are picked up by the twisted mucus string and this accounts for the dark color of the spiral structure. Nelson further suggests that, after an animal is starved, loses its style, and then suddenly starts feeding again, it usually regenerates a dark-cored new style. In the case of Adula falcata, continuous

feeding, with loss and subsequent regeneration of the style, as is probably the case in the subtidal situation as well as in aquaria, is the more common cause for the dark-cored style being produced. Doubtless, as Morton (1952) has suggested, it is advantageous to the style bearer to recycle food material which would otherwise be lost; but, on the other hand, the amounts of food involved in this process are probably too minute to be of any real importance to the animal's nutrition.

The crystalline style functions in supplying most, but not all, of the digestive enzymes found in the lumen of the stomachs of style bearing bivalves (Reid, 1968). According to Morton (1966), the style acts as a stirring rod and windlass as well. I found no evidence of the crystalline style of Adula falcata functioning as a windlass for the string of mucus-bound food emerging from the posterior end of the oesophagus. The physics of Morton's observation suggest that there would have to exist some mechanism for increasing the rate of the food string moving down the oesophagus as the bolus of material around the style increased in diameter. Otherwise, as the first wrappings were going on the style, there would be a windlass mechanism, but, as the bolus diameter increased, so would the rate of wrapping increase (if one can assume that the rate of the rod's turning is constant) and the food string would break from the strain. Another possibility is that, as the food bolus increases in diameter, increased friction with the walls of the stomach would act as a clutch, slowing the turning rate of the style and, thus, keep the wrapping speed of food strings

uniform.

My observations on conditions associated with the acceptance or rejection of particulate material in Adula falcata (Table I) suggest that its sorting mechanisms are not highly efficient. However, permitting the passage of some sediment material into the stomach could be advantageous to the animal's well-being. The presence of sediment matter in the gut may aid trituration of food, as is the case in tellinids (Yonge, 1949). More likely, the consolidation of sediment particles into firm faecal pellets prevents reintroduction of that material into the mantle cavity or burrow. Reid and Reid (1969) report a sand-grain epiflora in the stomach of Macoma secta which comprises most of its nutrients. Since fine sediment particles would posses a surface area proportionally higher than that of sand grains, it is possible that the small amount of sediment material in the stomach of Adula falcata provides nutritional value as well.

Adaptive radiation of the bivalve foot is illustrated most commonly in the function of locomotion. The creeping of the saddle oyster Enigmonia aenigmatica (Yonge, 1957), Lasaea rubra climbing a rock face by means of adhesion to a slime trail (Morton, 1960), and the leaping and digging in of cockles are all executed by the animals' use of the foot. Within the group of rock boring bivalves, if the foot is functional at all, it is utilized for stabilization of the visceral mass during boring, either by the laying-down of a byssus, in the case of Adula (Botula), Lithophaga, and Tridacna (Yonge, 1955 and 1936), or in functioning as a sucker, gripping the head of the burrow, as reported by

Purchon (1955b) for the Pholadidae. In Adula falcata the foot performs the additional function of cleansing its burrow walls of the particulate mudstone produced during mechanical boring.

VIII. SUMMARY

1. The ciliary currents of feeding and digestion in Adula falcata are figured and discussed in terms of their relationship to sediment removal.

2. It was observed that the mantle folds form a "functional" inhalant siphon while large amounts of sediment material are being removed from the mantle cavity via the inhalant siphon.

3. The finer sediment materials which get by the sorting mechanisms of the mantle cavity are taken into the alimentary tract and, following sorting by the ciliary mechanisms of the stomach, are consolidated into faecal pellets by the intestine.

4. Observations made on a specimen of Adula falcata living in a transparent "Bioplastic" burrow revealed that much of the sediment matter lining the walls of the boring is removed by the ciliated surface of the bivalve's unusually extensible foot.

5. It is suggested that the selection or rejection of particulate matter by Adula falcata is made solely on the physical basis of the size, density, and mucus-bound state of the particles.

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